The use of tree-fall gaps by a forest interior avian frugivore in a tropical evergreen forest

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Previous studies suggest that forest birds commonly use tree-fall gaps owing to the relatively higher availability of fruits and arthropods. However, others have argued that gaps may not be important for food resources but may offer other services, such as increased protection from predators owing to denser vegetation associated with gaps. We examined the use of tree-fall gaps by Puff-throated Bulbul *Alophoixus pallidus*, an abundant generalist frugivore found in tropical evergreen forests of East Asia. Bulbuls (family Pycnonotidae) are known to be the most important small frugivores in this region (an area with the highest rate of deforestation in the world), and likely to be integral to regional forest maintenance as well as regeneration. This bulbul did not preferentially use small gap interiors (average 163 ± 43 SE m²) and probably avoided them, but it appeared to use areas immediately surrounding gaps more than expected particularly during the breeding season. Such areas probably provide increased security for roosting adults and for young fledglings during the post-fledging period. This first detailed study of the movement of forest bulbuls in tropical East Asia suggests that the use of gaps and gap edges by these frugivores is highly variable in space and time (with equally complex reasons for their use or avoidance) but is likely to impact their role in forest maintenance and restoration.

INTRODUCTION

Differences in age, size or location of tree-fall gaps—defined by Brokaw (1982) as vertical holes in the forest extending from canopy level down through a height of 2 m above ground—can greatly impact the distribution and abundance of animals by influencing the availability of resources (Fogden 1972). Here we focus on gaps created through tree-fall or large branch-fall owing to wind storms or other natural processes, excluding fire, rather than those caused by human factors. Several initial studies suggested that frugivorous birds foraged more frequently in gaps relative to forest interior sites, presumably because gaps provided greater fruit (as well as arthropod) resources. Additional light levels in tree-fall gaps have been suggested to cause understorey shrubs and lianas to produce more fruits; gaps also provide more foliage in the understorey for herbivorous invertebrates and higher near-ground temperatures, which can also be more suitable for a variety of forest arthropods (Blake & Hoppes 1986, Levey 1988, 1990, Malmborg & Willson 1988). These studies also suggested that birds may change their foraging behaviour to increase fruit and arthropod foraging in gaps depending on the availability of resources (Blake & Hoppes 1986). However, more recent detailed studies of gaps and food resources suggest that there is a complex relationship between gap age and use by birds, and that many birds do not appear to track resources tightly in gaps at least at the scales measured (Restrepo *et al.* 1999). Nevertheless, regenerating gaps may provide other services for birds, particularly protection from predators owing to the density of vegetation (Anders *et al.* 1998, Bowen *et al.* 2007).

The aim of this study was to investigate whether a common frugivorous bird would preferentially use canopy gaps during the course of a year and whether such preferential use was related to food resources or other resources, particularly cover. We focused on a forest bulbul because of the importance of bulbuls as seed dispersers in East Asian forests (Corlett 1998) and because little is known about the movements of forest bulbuls. Furthermore, South-East Asia has the highest deforestation rate in the world (Sodhi & Brook 2006), so understanding the movement patterns of potential seed dispersers such as these will be fundamental in maximising the restoration potential of the region's forests. We assessed (1) whether Puff-throated Bulbuls *Alophoixus pallidus*, a locally abundant forest species, would spend proportionately more time foraging in natural tree-fall gaps or areas immediately surrounding gaps (referred to here as 'buffer' areas) compared to areas away from gaps, and (2) whether they would utilise gaps or buffer areas for resources other than food.

METHODS

The study was conducted in the 30-ha Mo-singto Long-term Biodiversity Research Plot (14°26′N 101°22′E), Khao Yai National Park (~2000 km²) in north-eastern Thailand. The plot consists of a series of ridges and valleys with an elevation range of 730–860 m asl. The vegetation is mostly mature evergreen forest dominated by fleshy-fruited trees with a ~0.25 ha section of secondary forest at the north edge of the plot (Brockelman 1998). The plot is laid out on a 20 m-square grid. All trees with diameter at breast height (DBH) ≥1 cm have been identified, labelled with unique ID numbers, and mapped using GIS with a precision ±1 m (Brockelman 1998). When the birds are seen, the tree numbers were used to reference their locations precisely.

One hundred and sixty-nine species of bird are known to occur on the plot (Round *et al.* 2011), with Puff-throated Bulbul having the highest density (>3 individuals/ha) (Gale *et al.* 2009). Puff-throated Bulbul is a common resident of evergreen forest of northern and north-eastern Thailand (Lekagul & Round 1991), and studies from Khao Yai suggest that it is also the commonest avian frugivore (Kitamura *et al.* 2002, Sankamethawee *et al.* 2011) and consumes the widest variety of fruits, based on faecal samples (80 plants species from185 samples) and direct observations of fruiting plants (>100 species between 2003 and 2008) (Sankamethawee *et al.* 2011). It forages in the lower to middle canopy with an average foraging height of 9.4 m (range 1–15 m) (P. D. Round *et al.* unpubl. data), in pairs or in groups of 3–7 birds (Sankamethawee *et al.* 2009), with an average home range of c.2.2 ha (Tanasarnpaiboon 2008). Birds also occasionally join mixed-species bird flocks feeding on insects (McClure 1974, Nimnuan *et al.* 2004). Their breeding season extends from February to July (Pierce *et al.* 2004). Colour-banding was initiated in January 2003 such that at the time of this study all family groups (31–32 groups) and the majority of individuals (~300 individuals) on the Mo-singto plot could be individually identified. As far as we are aware no quantitative habitat selection data are available for Puff-throated Bulbul, and while generally considered a forest species (Lekagul & Round 1991) it has been observed foraging along forest/non-forest edges (Chaikuad 2000). Furthermore, Bowen *et al.* (2007) found that many species generally classified as forest-interior species were frequently observed in forest gaps, often depending on season.

Vegetation was classified into three categories: tree-fall gaps, gap buffer areas (0–10 m from the gap edge) and forest interior.

All the gaps in our study plot were created by natural tree-falls. We used a somewhat narrower definition of a tree-fall gap than Brokaw (1982): following Wongsriphuek (2008), who mapped gaps on the Mo-singto plot just prior to the start of this study, we defined gaps as open areas larger than 25 m^2 and covered by vegetation shorter than 5 m. Gap edges were marked with plastic stakes at 1 m intervals. Tagged trees on the edge of gaps were used to georeference the gaps. The coordinates were mapped in a GIS (ArcView 3.2a) to create polygons for each gap and to estimate their area. The 10-m buffers around these gaps were drawn in ArcView 3.2a using the Buffer Selected Features command in the XTools extension.

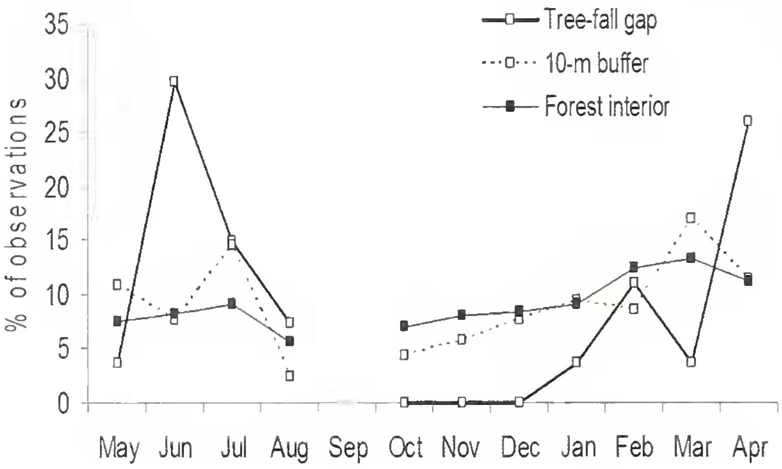
We selected ten groups of Puff-throated Bulbul which occupied c.20 ha of the core of the 30 ha Mo-singto plot, and precisely mapped their movements using the georeferenced trees. All activities of the ten selected groups were recorded to determine if they spent proportionately more time in gaps, near gaps or away from gaps in the surrounding forest. The ten selected groups were followed two hours twice per month from May 2007 to April 2008 (for logistical reasons no data were collected in September 2007). The observations started when at least one individual in a group was located. The behavioural data to examine the response to gaps were taken from the second hour of each of the two-hour observations to avoid possible biases relating to greater initial detection in gaps. Observations on a particular group were distributed evenly throughout the day to avoid potential biases associated with time of day. Behavioural data were grouped into two seasons: breeding (February–July) and non-breeding (August–January), which included feeding (on both fruit and arthropods), breeding (nest building, incubating, brooding and feeding offspring) and roosting (perching, calling, preening and resting). To test the frequency of gap and non-gap use, as well the frequency of the different behaviours between breeding and non-breeding seasons, Fisher's exact tests were carried out using R version 2.11.0. Total use areas were based on minimum convex polygons drawn around each of the ten groups using the Minimum Convex Polygon command in ArcView 3.2a for estimating the expected use. We used the ratios of observed *vs* expected observations per group per habitat to examine the overall trends within and among habitat types. To generate the expected values we used the areal proportions of each habitat type for each group multiplied by the number of observations of each group in each of the three habitat types.

RESULTS

There were 28 gaps (average 163±43 SE m^2) within the home ranges of the ten selected groups of Puff-throated Bulbul (mean 2.8±0.57 SE gaps/group), totalling 0.5 ha. The percentage areas covered by gaps, 10-m buffers and interior forest were 2.09%, 10.05% and 87.86% for the total area occupied by the ten groups. Based on the Mo-singto tree database, as expected most of the older gaps were covered by a dense layer of herbaceous seedlings and saplings, but had few trees with DBH ≥1 cm (0.1 trees/m^2). The 10-m buffer areas were more densely vegetated (0.4 trees/m^2) and tree crowns were typically covered with a dense tangle of lianas. A study of lianas on the Mo-singto plot also indicated that the number of lianas was higher in gap areas (gap interiors and gap-edges) than the primary forest (Wongsriphuek 2008). The database also indicated that the forest interior had the highest tree density (0.6 trees/m^2).

Overall, 84.56% of the observations occurred in the forest interior (n = 2,120), while the proportion of observations of bulbuls in tree-fall gaps was 1.08% (n =27) and in the 10-m buffers 14.36% (n = 360). The use of gaps and 10-m buffer areas tended to vary with time. Of the observations in tree-fall gaps, the largest percentage occurred in June (30%) (n = 7) and none in October–

Figure 1. The precentage of observations of Puff-throated Bulbul activities in tree-fall gaps (n = 27), 10-m buffers surounding gaps (n = 360) and the forest interior (n = 2,120) as a percentage of the total number of observations in each particular habitat based on the total number of observations of ten different groups in each particular habitat over an 11-month period (May 2007–April 2008).



December (Fig. 1). The number of observations in tree-fall gaps was more frequent during the breeding season (February–July). The highest percentage of observations in the buffer areas was during March (17%) (n = 61), the lowest in August (3%) (n = 9) (Figure 1). The number of observations in the forest interior fluctuated relatively little during the study period (Figure 1). Overall, there were 1,579 observations obtained during the breeding season and 928 during the non-breeding season. For all groups combined, Puff-throated Bulbuls used the gaps, 10-m buffers and forest habitat differently between breeding and non-breeding seasons (Fisher's exact test, $p < 0.001$) (Table 1 and below). When analysed separately by group, this difference was significant between seasons for only two groups; however, the other groups seem to have similar patterns (Table 1).

Approximately 65.75%, 32.01% and 2.24% of the behaviours were associated with roosting, feeding and breeding respectively. There were significant differences in behaviour among habitats for all groups combined (Fisher's exact test, $p < 0.001$) (see below). When analysed separately by group, behaviours were also different among habitats for four of the ten groups (Fisher's exact test, p = 0.01–0.03). Nine out of ten groups appeared to use gaps less than expected (ratios were less than one), with three groups having no detections in the gaps (Table 1). There was only one group that appeared to use gaps more than expected (ratio was greater than one), especially during the breeding season. The remaining groups appeared in gaps more often during the breeding season but still lower than expected overall (Table 1). In contrast, seven out of ten groups used the 10-m buffer areas more than expected (ratios were greater than 1), mostly for roosting and feeding, while two groups appeared to use the buffer areas less than expected. Puff-throated Bulbul was detected more often in the buffer areas during the breeding season than non-breeding season (252 *vs* 108 observations). Although there were more hours of observation during the breeding than the non-breeding season (12 *vs* 10 hours per group), with an expected ratio of 6:5 for total observations, there were 5.8 and 2.3 times more observations in the gaps and buffer areas during the breeding season than the non-breeding season respectively (Table 1). However, the magnitude of the overall seasonal difference in gap use was somewhat skewed owing to the relatively frequent use by one group during the breeding season. There was no particular behaviour associated with the use of buffer areas.

For the forest interior there were no trends among the different behaviours or between seasons. There was only one group that occurred in the forest interior less than expected (Table 1).

Table 1. Use of tree-fall gaps, 10-m buffer zones surrounding gaps and forest interior by Puff-throated Bulbul from May 2007 to April 2008. The breeding season (BR) is during February–July and the non-breeding (NB) August–January. The ratio refers to the ratio of observations per group per habitat to expected observations. Expected observations were generated from the areal proportions of each habitat type for each group multiplied by the total number of observations of each group in all habitats. The total expected observations were generated from the proportions of each habitat type across all home ranges multiplied by the total number of observations of all groups in all habitats. Based on the total number of hours of observation during each season, the expected ratio of breeding to non-breeding season observations was approximately 6:5.

	Gap					Buffer					Forest				
	Season					Season					Season				
Group	BR	NB	No. of observations	Expected no. of observations	Ratio	BR	NB	No. of observations	Expected no. of observations	Ratio	BR	NB	No. of observations	Expected no. of observations	Ratio
1	2	0	2	4.7	0.42	50	36	86	28.3	3.04	81	67	148	203.0	0.73
2	13	2	15	10.5	1.43	34	17	51	42.5	1.20	121	63	184	197.0	0.93
3	2	0	2	2.5	0.81	16	6	22	14.8	1.48	142	81	223	229.7	0.97
4	1	0	1	1.5	0.65	2	2	4	14.0	0.29	139	75	214	203.2	1.05
5[a]	2	0	2	2.2	0.92	31	6	37	21.8	1.70	110	69	179	191.8	0.93
6	3	0	3	4.5	0.66	45	8	53	29.5	1.80	100	71	171	193.0	0.89
7	0	0	0	4.2	0.00	18	8	26	27.4	0.95	97	88	185	179.4	1.03
8	0	2	2	2.7	0.73	22	14	36	13.7	2.63	143	92	235	257.6	0.92
9	0	0	0	3.2	0.00	2	4	6	19.4	0.31	204	113	317	300.4	1.06
10[a]	0	0	0	4.2	0.00	32	7	39	34.2	1.14	167	97	264	264.5	1.00
Total	23	4	27	52.0	0.52	252	108	360	251.0	1.43	1304	816	2120	2,193.0	0.97

[a]Groups which used habitat types differently between breeding and non-breeding seasons (Fisher's exact test, $p < 0.05$)

Although breeding behaviours did not occur significantly more often in gaps or 10-m buffer areas, of the 56 observations associated with breeding, 26 (46%) occurred during the post-fledging period. Eight percent occurred in gaps, 19% in the 10-m buffer areas and 73% in the forest interior. Thus, while more than 25% of the breeding-associated observations were related to caring for fledglings in or adjacent to gaps, the proportion was not significantly different from expected ($\chi^2 = 3.7, p = 0.057$), although suggestive of greater use of gaps and buffers for fledgling care. Of the seven groups that successfully produced fledglings, three were observed utilising gaps or 10-m buffer areas with their fledglings. In the forest interior the number of observations during the post-fledging period was not significantly different from expected ($\chi^2 = 0.37, p = 0.54$).

DISCUSSION

Overall, there were only 27 observations of Puff-throated Bulbuls using gaps out of >2,500 total observations, suggesting there was no preference for gaps, and perhaps gap avoidance, with the frequency of gap use being significantly lower than expected ($\chi^2 = 12.02, p < 0.001$; Table 1). During the non-breeding season, Puff-throated Bulbuls were detected in gaps much less than expected. Most of the detections in the gaps occurred during the breeding season. Overall only one group out of ten appeared in the gaps more than expected, while the other nine groups used them less than expected, including three which were never observed to use gaps. These results are in agreement with Bowen *et al.* (2007), who suggested that forest bird use of gaps was seasonal and, depending on species, more or less common than expected. For these bulbuls open gaps may present a greater risk from predators (Willson *et al.* 1982, Belisle & Desrochers 2002). Although we did not determine the exact ages of the gaps, Puff-throated Bulbuls tended to care for fledglings in older gaps where there was more vegetation cover.

Overall, the 10-m buffer areas appeared to be particularly important locations for roosting and feeding year-round, presumably owing to the dense cover and density of food resources. Regenerating gaps and areas immediately surrounding gaps were covered by dense vegetation, especially lianas, at the gap edges rather than in gap interiors. Puff-throated Bulbul preferred to roost during the day in areas adjacent to gaps where there was probably greater cover and where they seemed to spend more time feeding fledglings as well, presumably to reduce the risk from predators, especially raptors (Anders *et al.* 1998, Belisle & Desrochers 2002, Bowen *et al.* 2007).

While it is not possible to generalise from one species, this paper and Khamcha *et al.* (2012) represent the first detailed studies of the movement of forest bulbuls in tropical East Asia, and suggest that the use of gaps and gap edges by bulbuls is probably highly variable in space and time and the reasons for their use or avoidance equally complex and probably dependent on the type of resource that the gap and the surrounding habitat provides. Based on our observations, the Puff-throated Bulbul probably contributes little to forest gap regeneration, but rather to the overall maintenance of forest interiors. Other forest bulbuls are worth investigation, as at least some are highly likely to prefer gaps and therefore may be significant contributors to the regeneration of fragmented forests in the region.

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